

Emergence of Overwintered Boll Weevils (Coleoptera: Curculionidae) in Relation to Microclimatic Factors

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ABSTRACT The boll weevil, *Anthonomus grandis* Boheman, enters a diapause state to survive winters in temperate regions and subsequently emerges from overwintering habitats to infest squaring cotton in the spring. Previous research has found that boll weevil overwintering emergence is closely associated with climatic patterns of temperature and precipitation. The objectives of this study were to determine the effects of temperature, humidity, and other meteorological factors on the temporal pattern of boll weevil emergence, and to compare the physiological and morphological conditions of emerged and trapped weevils. Emergence cages were infested with diapausing weevils in the fall. Daily emergence and microclimatic conditions of the leaf litter and air were monitored until the subsequent summer. Air temperature and relative humidity, incident solar radiation, and precipitation were significantly greater on emergence dates than on dates with no emergence. Emerged and trapped weevils were dissected to assess their morphology. Emerged weevils tended to exhibit greater fat body development, a higher frequency of testicular atrophy, and less ovary development than trapped weevils. None of the emerged weevils were rated extra lean and no trapped weevils were rated fat. These results are consistent with previously-reported effects of climatic factors on weevil emergence in other areas of the Cotton Belt, and add new information about the physiological and morphological characteristics of emerged weevils. This information on the dynamics and mechanisms of overwintering provides insight that should be helpful in formulating improved predictive models, risk assessments, and management strategies for the boll weevil.

KEY WORDS overwintering, emergence, microclimate, boll weevils

THE ADULT BOLL WEEVIL, *Anthonomus grandis* Boheman, enters a state of dormancy (diapause) that contributes to its ability to survive winters in temperate regions (Brazzel and Newsom 1959). Adult boll weevils emerge from overwintering habitats in the spring and subsequently infest squaring cotton. The temporal pattern of emergence of weevils from overwintering is influenced by their physiological condition and the climatic conditions of their overwintering habitats (Rummel and Summy 1997).

Overwintering weevils use habitats that moderate adverse climatic conditions for several months before emergence. Although deciduous leaf litter has been reported as their primary overwintering habitat, boll weevils are known to use a variety of overwintering quarters. Beckham (1957) found overwintering weevils in pine straw from wooded areas near cotton fields in Georgia. Bondy and Rainwater (1942) reported that weevils successfully overwintered beneath ground cover comprised of Spanish moss or corn stalks. Boll weevils may also overwinter within cotton bolls on the

ground (Cowan et al. 1963), in stands of weeping lovegrass (Brown and Phillips 1989), and in Conservation Reserve Program grasses (Carroll et al. 1993). Graham et al. (1978) found hackberry, granjeno, and grassy areas to be the three primary overwintering habitats in the subtropical Lower Rio Grande Valley of Texas. Winter habitats modify the microclimate experienced by overwintering weevils. For example, Parajulee et al. (1997) reported that average daily minimum temperatures were 3–6°C greater and average daily maximum temperatures were 4–6°C less than the respective air temperatures in shinnery oak, mesquite-grass pasture, pecan, and shelterbelt habitats.

Several studies have related overwinter survival and timing of emergence to temperature and precipitation patterns. Parajulee et al. (1996) found that higher temperatures were associated with earlier initiation of spring emergence. Parencia et al. (1964) reported higher early-season infestations of fruiting cotton when maximum temperatures exceeded 21.1°C and during months with appreciable precipitation. The influence of moisture on emergence appears to increase as temperatures increase (Mitchell et al. 1972). Also, shade afforded by leafy canopies reduces inso-

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lation and heating of overwintering habitats, and increases the variability of the microclimate and emergence patterns of boll weevils (Slosser et al. 1984a, 1984b; Slosser and Fuchs 1991).

Captures of weevils in pheromone traps have been used to estimate boll weevil emergence patterns. White and Rummel (1978) compared patterns of captures in pheromone traps with counts of weevils in cotton fields and concluded that emergence from overwintering began several weeks before cotton was colonized. Carroll and Rummel (1985) found a strong correlation between the period of peak emergence from overwintering and peak response to pheromone traps. However, these studies did not examine the physiological and morphological characteristics of the emerged and trapped weevils. Our objectives were to determine the effects of temperature, humidity, and other meteorological factors on the temporal patterns of boll weevil emergence, and to compare the physiological and morphological conditions of emerged and trapped weevils.

Materials and Methods

Weevil-infested squares were hand picked from fruiting cotton fields. The infested squares were divided among several $20 \times 20 \times 20$ -cm screened Plexiglas cages with ≈ 300 infested squares per cage. The cages were held in environmental chambers at 29.4°C and a photoperiod of 13:11 (L:D) h. The cages were inspected daily and newly emerged adults were removed. At the onset of adult emergence, infested squares were misted daily with reverse-osmosis water to soften the squares and facilitate weevil emergence. Approximately 300 weevils were held in each of several cages identical to those used for rearing. Plexiglas cages were held in the laboratory at room temperature ($\approx 24^\circ\text{C}$). Adult weevils were provided a source of reverse-osmosis water and fed at a rate of one small debracted boll (17–25 mm diameter) per 10 weevils for 3 wk after the first adults emerged. Bolls were replaced three times weekly (Mondays, Wednesdays, and Fridays). All weevils used in the study emerged within a 5-d period (6–10 October 1999). Dead weevils were removed when the bolls were replaced.

After the 2- to 3-wk feeding period, weevils were sexed according to the methods of Sappington and Spurgeon (2000) and marked to identify the gender of the cohort group. An aliquot of 25 weevils was dissected to determine the proportion of weevils expressing diapause characteristics.

Pyramidal field emergence cages were constructed of a galvanized metal frame and steel window screening, and had a 1-m^2 basal area. Cages were placed over relatively undisturbed deciduous leaf litter ($\approx 1\text{--}2$ cm deep) in a wooded area near the bank of the Brazos River, Burleson Co., TX. Twenty cages were deployed in fall 1999. Each emergence cage was infested with 50 randomly selected marked weevils (25 males and 25 females) on 30 October 1999 and sealed with an opaque lid until 13 January 2000 to induce weevils to overwinter within the leaf litter.

A Campbell Scientific (Logan, UT) 21XL datalogger, AM416 multiplexer, and CR10 datalogger were used to record hourly meteorological data at the emergence site. Thermocouples (24 AWG; Omega Engineering, Stamford, CT) were placed within each cage on 29 October 1999 to measure air and leaf litter temperature. Honeywell (Morristown, NJ) HIH-3605 humidity sensors were deployed on 29 October 1999 to measure relative humidity of the leaf litter within eight emergence cages. A thermocouple (and a humidity sensor when applicable) were placed at the interface between the soil and leaf litter within each cage. A second thermocouple was shielded by an inverted white plastic cup with a black-painted interior at a height of 0.3 m within each cage. Hourly measurements of ambient air temperature, soil temperature, ground surface temperature, relative humidity, barometric pressure, solar radiation, and precipitation were also recorded at a central weather station. Hourly meteorological data were summarized over 24-h periods beginning at 1200 hours CST to coincide with daily examination of the emergence cages. Degree-days above a threshold of 6.1°C (Parajulee et al. 1996) were calculated for the leaf litter ($\text{DD}_{\text{litter}}$) and air (DD_{air}). Cumulative degree-days ($\text{CDD}_{\text{litter}}$ and CDD_{air} for leaf litter and air, respectively) and precipitation (CP) after 1 November 1999—the first complete day of climatic measurements—were calculated as predictors of cumulative weevil emergence.

Groups of four cages were clustered into treatment groups. Treatments consisted of greenhouse enclosures without artificial heating (GR4), and with heating to a constant air temperature of 15°C (GR3), 20°C (GR2), and 25°C (GR1). Greenhouses were constructed of clear plastic sheets draped over an arched framework of PVC pipes, with a maximum height of ≈ 1.2 m. Plastic sheets were sealed at the base of the framework with 2.44-m lengths of $0.05 \text{ m} \times 0.10 \text{ m}$ lumber. Plastic sheets were opened only to inspect the cages and heaters within each greenhouse. Greenhouse heating systems consisted of a Vornado EH1-0005 (Air Circulation Systems, Wichita, KS) vortex electric heater, a Duracraft CZ-320 (Duracraft, Southborough, MA) oscillating electric heater, a Lasko 2009 (Lasko Metal Products, West Chester, PA) oscillating fan, and a bimetallic thermostat, which were operated to maintain desired air temperatures. A Miller Bobcat 225 (8500-W peak power; Miller Electric Mfg., Appleton, WI) gasoline-powered generator supplied power to the greenhouse heating system. An unheated and uncovered set of ambient (AMB) cages was also maintained. Greenhouses were operated continuously from 24 January 2000–14 February 2000, when daily minimum air temperatures were forecast to be $<10^\circ\text{C}$.

A single boll weevil pheromone trap was deployed on the margin of the wooded area and ≈ 200 m north of the emergence cages. The trap was baited with a new 10-mg grandlure bait (Plato Industries, Houston, TX) every 2 wk. Opaque lids were replaced with steel screen funnels enclosed by 237-ml clear glass jars on 13 January 2000. Emergence cages and the pheromone

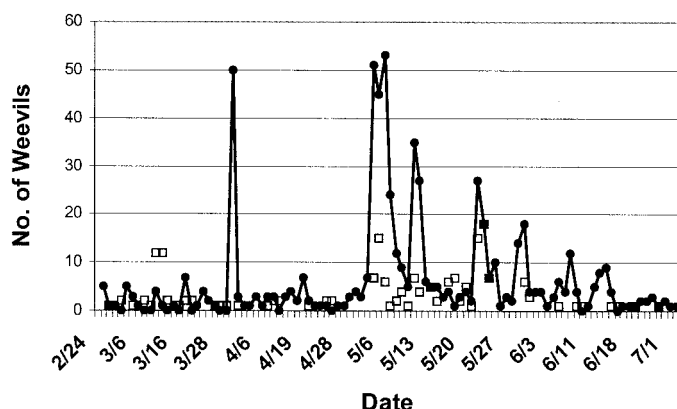


Fig. 1. Daily capture of boll weevils in pheromone traps (squares) and overwintering emergence cages (solid circles) at the Brazos River site, Burleson Co., TX, 24 February to 1 July 2000.

trap were inspected daily at ≈ 1300 hours CST from 11 January to 10 July. When emergence cages were examined, weevils visible on the sides of the cages were removed in addition to those in the collection jars. Collected weevils were stored in a refrigerator and dissected on the day of collection, except for a total of four weevils on 28 March, 8 April, and 21 April that were dissected the following day, and one crushed weevil on 29 March that was not dissected.

Fat body ratings were based substantially on descriptions provided by Brazzel and Newsom (1959). Weevils were classified as fat if the fat body obscured most of the internal organs, intermediate if the fat body was well developed but portions of the digestive tract or reproductive organs were generally visible, and lean if internal organs were generally visible, regardless of presence of fat. Reproductive characters were assessed in dissections according to the methods of Spurgeon and Raulston (1998). Ovaries were rated according to the presence or absence of previtellogenic oocytes, oocytes containing yolk, and mature (chorionated) eggs. Testis rating was classified as pre-reproductive if the testes were translucent, early-reproductive if the testes had opaque centers and translucent lobes, late-reproductive if the testes had opaque centers and cloudy lobes, or atrophied if the testes were opaque because of dense deposits of yellow fat.

Dissection data for emerged and trapped weevils were merged with climate data by day-of-year, greenhouse, and cage. Mean differences in sex ratios of emerged weevils among greenhouses were tested for significance using analysis of variance (ANOVA) (PROC GLM; SAS Institute 1988). Mean differences of air temperature, leaf litter temperature, and leaf litter relative humidity among emergence cages were tested for significance using ANOVA and separated using the Waller-Duncan K-ratio *t*-test (PROC GLM; SAS Institute 1988). Mean differences of daily climatic factors for emergence dates and dates with no emergence were tested using the *t*-test statistic (PROC TTEST; SAS Institute 1988). Cumulative percent emergence, cumulative degree-days, and cumulative

precipitation were calculated for each emergence cage. The set of cumulative values was pooled to compute statistical relationships. Cumulative percent emergence (CE) was fitted with CDD_{litter} , CDD_{air} , CP, and day-of-year (DOY) by stepwise linear regression (PROC REG; SAS Institute 1988) using a selection level of significance of 0.05 for entry of variables into the regression equation and was tested for significance using the F-statistic. Because of the infrequent occurrence of some physiological and morphological conditions, physiological and morphological factors were each pooled into two classes for contingency tables that could be tested using the Fisher Exact Test (PROC FREQ; SAS Institute 1988). Fat body ratings were reclassified as hypertrophied (intermediate or fat) or normal (extra lean or lean). Testis rating was reclassified as atrophied or not atrophied. Statistical differences were interpreted using individual cell contributions to the χ^2 value (CELLCHI2 option of PROC FREQ).

Results

Emergence Patterns

Weevils emerged on 87 dates over a period of 128 d from 24 February to 1 July (Fig. 1). The mean cumulative emergence of all cages occurred on a mean (\pm SEM) day-of-year (DOY) of 128.6 ± 1.4 d (i.e., 8 May) (Fig. 2). Weevils emerged from a single-day maximum of 19 cages on 29 March. Maximum daily emergence (53 weevils) occurred on 3 May. The greatest number of weevils emerged from the 25°C treatment cages (GR1) and the least from the uncovered and unheated cages (AMB) (Table 1). A total of 619 marked weevils emerged, and the remains of 159 weevils were recovered when the leaf litter was excavated on 10 July. Emergence of females ($N = 316$) did not significantly exceed the emergence of males ($N = 303$). The within-treatment range of total emergence among cages was greatest (10–45 weevils) for the covered but unheated cages (GR4) and least (30–41 weevils) for the 20°C treatment cages (GR2).

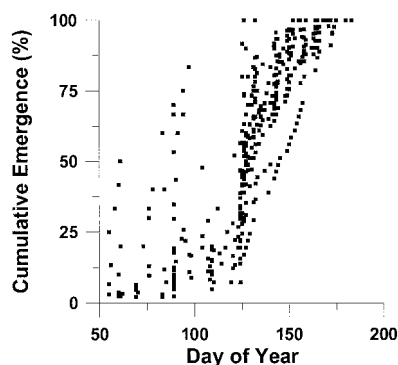


Fig. 2. Cumulative percent emergence for individual emergence cages versus day-of-year at the Brazos River site, Burleson Co., TX, 1 November 1999 to 1 July 2000.

During the emergence period, 183 weevils were captured in the single pheromone trap on 49 d. The pheromone trap captured a maximum of 15 weevils on 4 May. Daily capture of weevils in the pheromone trap were significantly related ($F = 66.5$; $df = 1, 168$; $P < 0.01$; $R^2 = 0.28$) to daily emergence of weevils using linear regression.

There were significant differences among cages in daily mean leaf litter temperature, air temperature, and leaf litter relative humidity between 1 November 1999 and 1 July 2000 (Table 2). However, mean daily minimum air temperatures were not significantly different among cages between 1 November 1999 and 1 July 2000.

Significant differences were observed between daily climatic factors associated with emergence dates and dates of no emergence, respectively (Table 3). Daily leaf litter temperatures were 4.4–4.9°C higher and air temperatures were 1.5–3.5°C higher on emergence dates than on dates of no emergence within emergence cages. Mean temperatures of the soil, ground surface, and air outside of the emergence cages were significantly higher on emergence dates than on dates of no emergence. Daily mean barometric pressure, mean relative humidity, total precipitation, and total solar radiation were significantly higher on emergence dates than on dates of no emergence. Mean weevil emergence among cages occurred at a

mean (\pm SEM) of $CDD_{litter} = 1922.2 \pm 30.0$ DD after 1 November 1999 (Fig. 3). Overall emergence started at $CDD_{litter} = 645.9$ DD and ended at $CDD_{litter} = 3510.7$ DD. Mean emergence occurred at a mean (\pm SEM) of $CDD_{air} = 1672.7 \pm 20.5$ DD after 1 November 1999 (Fig. 4). Emergence occurred from $CDD_{air} = 680.1$ to 2581.8 DD. A mean (\pm SEM) of $CP = 280.9 \pm 3.8$ mm was associated with the mean date of emergence (Fig. 5). Emergence occurred between 104.1 and 393.2 mm of accumulated precipitation. Cumulative percent emergence (CE) in all cages was related to CDD_{litter} , CDD_{air} , CP, and DOY according to the following multiple linear regression equation:

$$CE = -73.46 - 0.011 * CDD_{litter} + 0.034 * CDD_{air} + 0.041 * CP + 0.369 * DOY,$$

which was significant ($F = 302.6$; $df = 4, 305$; $P < 0.01$; $R^2 = 0.80$).

There was a statistically significant relationship ($F = 15553.1$; $df = 1, 6085$; $P < 0.01$; $R^2 = 0.72$) between DD_{litter} and DD_{air} , but with substantial variability (RMSE = 3.62). The correlation between DD_{litter} and DD_{air} decreased ($F = 96.9$; $df = 1, 371$; $P < 0.01$; $R^2 = 0.21$) when considering only the dates of actual emergence. Heterogeneity in both environments (especially leaf litter) resulted in considerable variation in these relationships even within a restricted area of habitat. This inherent variation will make further refinement of degree-day models of boll weevil emergence difficult, and probably limit wide applicability of such models.

Morphological Characteristics

The initial aliquot of weevils used to determine the proportion of diapause after the feeding period included 16 males and nine females. All of the males and eight of the females (96% total) exhibited diapause characters.

Significant differences in morphological characteristics were evident between the emerged and trapped weevils. Emerged weevils tended to have more substantial fat bodies (Fisher Exact Test, $P < 0.01$) than did weevils from the trap (Fig. 6). A greater proportion (85.6%) of emerged weevils had hypertrophied fat body than did trapped weevils (2.3%). According

Table 1. Total emergence of overwintering adult boll weevils from leaf litter at the Brazos River site, Burleson Co., TX, 24 February to 1 July 2000

Greenhouse	Heater setting	Males	Females ^a	Males:Females ^b	Total ^c	Percent of total released
GR1	25°C	71	75	0.947	146	73.0
GR2	20°C	70	72	0.972	142	71.0
GR3	15°C	58	57	1.018	115	57.5
GR4	—	64	61	1.049	125	62.5
AMB	—	40	51	0.784	91	45.5
Total	—	303	316	0.959	619	61.9

^a One unmarked female emerged on 3 May from GR3–4, but was excluded from the emergence count.

^b Sex ratios among the greenhouses were not significantly different ($\alpha = 0.05$) using ANOVA (PROC GLM; SAS Institute 1988).

^c Remains of 70 males and 89 females were recovered from leaf litter at the conclusion of the study on 10 July, but were excluded from the total counts.

Table 2. Daily mean climate statistics for 20 emergence cages in the boll weevil overwintering emergence study, Brazos River site, Burleson Co., TX, 1 November 1999 to 1 July 2000

Greenhouse	Cage	Heater setting ^a	Litter temperature (°C) ^b	Air temperature (°C) ^b	Litter relative humidity (%) ^b
AMB	1	–	19.1ef	15.9b	95.2c
AMB	2	–	21.6b	15.9b	96.5b
AMB	3	–	17.1gh	15.9b	94.6c
AMB	4	–	15.9i	15.9b	98.8a
GR1	1	25°C	22.6a	17.3ab	–
GR1	2	25°C	19.9cde	17.5a	–
GR1	3	25°C	19.3ef	17.2ab	–
GR1	4	25°C	20.4cd	17.2ab	79.2g
GR2	1	20°C	17.2g	16.8ab	–
GR2	2	20°C	17.3g	17.0ab	–
GR2	3	20°C	17.3g	17.0ab	92.9d
GR2	4	20°C	17.2g	16.9ab	–
GR3	1	15°C	18.9f	16.6ab	–
GR3	2	15°C	16.1i	16.7ab	91.0e
GR3	3	15°C	16.2hi	16.7ab	–
GR3	4	15°C	16.0i	16.7ab	–
GR4	1	–	20.7bc	16.1ab	89.4f
GR4	2	–	15.8i	16.1ab	–
GR4	3	–	18.7f	16.3ab	–
GR4	4	–	19.6def	16.1ab	–

^a Greenhouses were deployed from 24 January through 14 February 2000, and electric heaters were operated in GR1, GR2, and GR3. GR4 was enclosed in a greenhouse without heaters, and AMB was not enclosed in a greenhouse.
^b Column means with the same letter are not significantly different using the Waller-Duncan K-ratio *t*-test ($\alpha = 0.05$).

to the cell chi-squares, the majority of this difference was explained by the less than expected number of trapped weevils with hypertrophied fat bodies. The proportion of emerged weevils rated as intermediate or fat decreased throughout the emergence period (Fig. 7). The last weevil rated fat emerged on 29 May and the last weevil rated intermediate emerged on 19 June. None of the emerged weevils were rated extra

lean and none of the trapped weevils were rated fat. The single unmarked weevil that emerged on 3 May had an intermediate fat body rating, as did 80.7% of the marked emerged weevils. Emerged weevils (50.5%) were more likely to have atrophied testes than were trapped weevils (4.6%) (Fisher Exact Test, $P < 0.01$). Cell chi-squares indicated nearly half of this difference was contributed by the lower than expected number of trapped weevils with atrophied testes. Trapped weevils (20.6%) exhibited a greater propensity for having previtellogenic oocytes than did emerged weevils (0.6%), and a greater proportion of trapped weevils (8.3%) had oocytes with yolk than did emerged weevils (0.0%) (Fisher Exact Test, $P < 0.01$). No mature eggs were present in either trapped or emerged weevils.

Table 3. Daily climate statistics for dates with and without boll weevil emergence at the Brazos River site, Burleson Co., TX, 14 January to 1 July 2000

Variable	Mean ^a	
	Emergence dates	Dates of no emergence
Inside Emergence Cages		
Minimum leaf litter temperature (°C)	23.4	18.5
Maximum leaf litter temperature (°C)	26.6	22.2
Mean leaf litter temperature (°C)	24.8	20.1
Minimum air temperature (°C)	17.5	14.0
Maximum air temperature (°C)	26.2	24.7
Mean air temperature (°C)	20.9	18.4
Minimum leaf litter relative humidity (%)	87.2	88.7
Maximum leaf litter relative humidity (%)	89.5	91.6
Mean leaf litter relative humidity (%)	88.3	90.5
Outside Emergence Cages		
Minimum air temperature (°C)	19.5	15.0
Maximum air temperature (°C)	27.8	24.9
Mean air temperature (°C)	22.9	19.4
Mean 10-cm soil temperature (°C)	23.0	19.6
Mean ground surface temperature (°C)	23.0	19.5
Total solar radiation (kW m ⁻²)	1.27	1.22
Mean barometric pressure (kPa)	100.7	101.1
Mean relative humidity (%)	90.1	80.4
Total precipitation (mm)	3.7	1.7

^a All row means are significantly different ($\alpha = 0.05$) using the *t*-test statistic (PROC TTEST; SAS Institute 1988). The equal variance assumption was validated for each test.

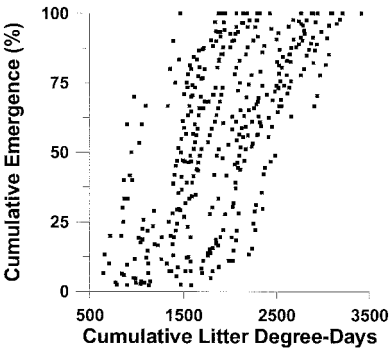


Fig. 3. Cumulative percent emergence for individual emergence cages versus cumulative degree-days (leaf litter temperature >6.1°C) at the Brazos River site, Burleson Co., TX, 1 November 1999 to 1 July 2000.

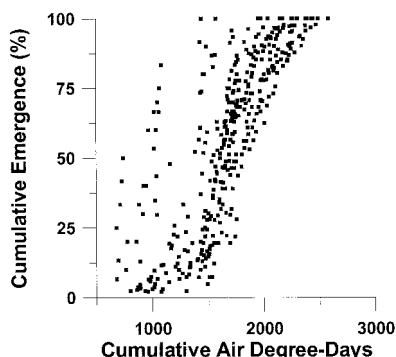


Fig. 4. Cumulative percent emergence for individual emergence cages versus cumulative degree-days (air temperature $>6.1^{\circ}\text{C}$) at the Brazos River site, Burleson Co., TX, 1 November 1999 to 1 July 2000.

Discussion

A number of investigators have used pheromone traps to estimate boll weevil emergence (Mitchell et al. 1973, Wade and Rummel 1978, Leggett et al. 1988, Fuchs and Minzenmayer 1990), and it is commonly accepted that patterns in spring trap captures reflect emergence patterns. Our results indicate that daily capture of weevils in the pheromone trap was significantly related with emergence of weevils in emergence cages, but peak values of these variables were often asynchronous. The divergence between emergence and trap capture patterns was most evident in the comparative pattern of peak values. Six of ten dates with either a trap peak or emergence peak were not characterized by paired peaks, as in the case of prominent peaks in emergence (50 weevils on 29 March) and trap capture (12 weevils on 9–10 March). These results suggest that although the general pattern of emergence may be reflected by trap captures, peaks in trap captures do not generally reflect corresponding peaks in the seasonal emergence profile.

Conclusions derived from our study regarding the relationship between emergence from overwintering

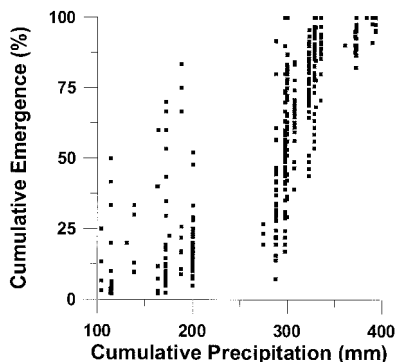


Fig. 5. Cumulative percent emergence for individual emergence cages versus cumulative precipitation at the Brazos River site, Burleson Co., TX, 1 November 1999 to 1 July 2000.

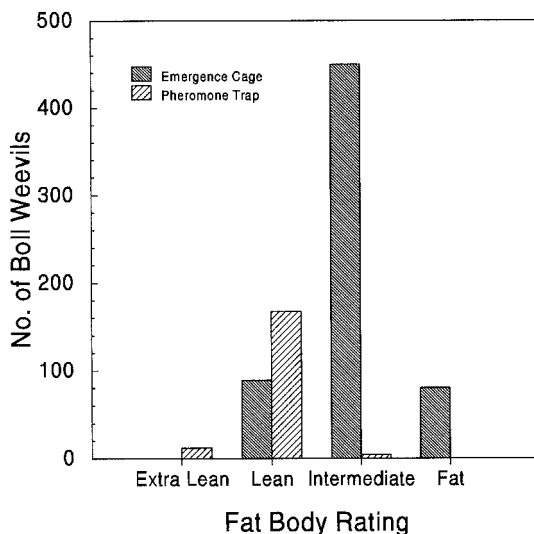


Fig. 6. Overall fat body ratings of boll weevils captured from overwintering emergence cages and pheromone traps at the Brazos River site, Burleson Co., TX, 24 February to 1 July 2000.

and the patterns of spring trap captures must be tempered by the fact that weevils removed from our emergence cages had more highly developed fat bodies than weevils captured in the trap. This difference may have resulted from one or more distinct scenarios. First, it is possible (and probable) that the weevils established in the emergence cages were generally better suited for overwintering survival than the bulk of weevils that enter overwintering quarters naturally.

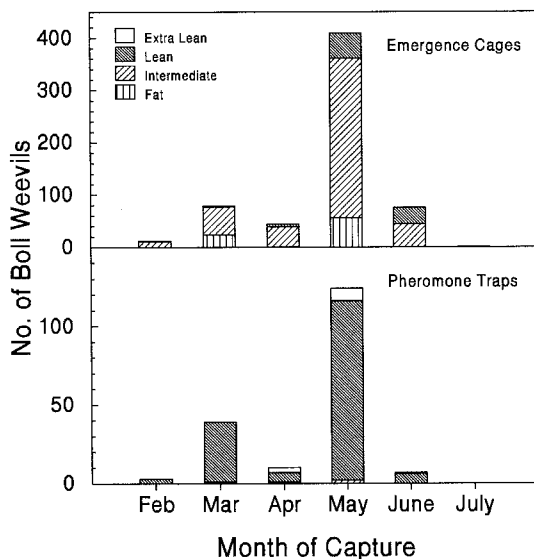


Fig. 7. Monthly fat body ratings of boll weevils captured from overwintering emergence cages and pheromone traps at the Brazos River site, Burleson Co., TX, 24 February to 1 July 2000.

In this case, based on the observations of Rummel et al. (1999) we would expect the poor survival of weevils with limited fat reserves at the time of entry into overwintering to moderate the influences of weevil condition on spring emergence pattern. Additional study will be needed to determine the extent of differences in fat reserves between weevils placed in overwintering habitat and those entering naturally. Second, the fat body ratings of weevils captured in traps may have been a reflection of their high activity (flight) since emergence. However, information regarding the rate of fat body depletion by flight activity that would lend insight into this possibility is not available. Finally, other investigators have observed weevils to reenter overwintering habitat after becoming active during the overwintering period (Gaines 1936, Reinhard 1943). Because our emergence cage study did not permit reentry, weevils that emerged and were dissected may have otherwise reentered the leaf litter to emerge again at a later date. If this were the case, the early emergence we observed would not necessarily constitute the "suicidal emergence" reported by Rummel and Carroll (1983).

Parajulee et al. (1996) related emergence patterns to degree-day accumulations but noted much unexplained variability in their model. These authors used a single temperature probe in each habitat. Our efforts to relate emergence patterns to degree-day accumulations also indicated substantial variability in this relationship despite the use of a separate temperature probe for each cage. This variability combined with our observations of the profound influences of precipitation on emergence may indicate degree-day accumulations either play a minor role in determining emergence patterns or represent only one of several mechanisms interacting to determine the temporal pattern of emergence. Our results demonstrate that short-term meteorological conditions greatly influence emergence patterns without respect to degree-day and precipitation accumulations. In addition, we exercised great care to ensure uniformity in the physiological condition of caged weevils as indicated by the high survival rates. We would expect less uniformity in a naturally overwintering population as this source of variation may further modify the observed emergence pattern.

Although our results indicate a relationship between spring emergence and ambient or leaf litter temperatures, the seven major emergence peaks highlight a more marked relationship between boll weevil emergence from overwintering and discrete rain events. In this respect, our results are very similar to those of Gaines (1935), who reported on 15 yr of emergence experiments in which 82.1% of weevils emerged within 7 d of rainfall ≥ 0.25 mm (0.01 inch) with 37.6% emerging on the day of rain and the following day. The observations of Reinhard (1943), that emergence decreases and may cease entirely during protracted dry spells, are also consistent with our results. Failure to adequately recognize or account for the dramatic influence of rainfall on the timing and extent of emergence may explain the inconsistent and

generally unsatisfactory predictions yielded by several previous efforts to model emergence (Leggett et al. 1988, Stone et al. 1990, Parajulee et al. 1996). It should also be recognized that the patterns we observed may not be indicative of emergence patterns in arid or semiarid production regions in which rain events during the emergence period are infrequent.

Our results indicated that most emergence occurred after late April, and that the amplitude of the emergence peaks tended to decrease with increased time. The timing of the earliest substantial emergence corresponded with the occurrence of a hailstorm on 1 May. Damage from the hailstorm to trees in the study area substantially reduced canopy shading and increased the penetration of solar radiation to heat the ground surface. This heating likely promoted the substantial increase in weevil emergence observed after this date. The decreasing amplitude of the emergence peaks after peak emergence appeared to be an artifact caused by population sampling without replacement rather than a reflection of the strengths of stimuli eliciting emergence behavior on the different dates.

Significant microclimatic differences in overwintering habitats and their effects on overwintering emergence of boll weevils have been presented. This bioclimatic relationship would better explain variability of estimated emergence patterns compared with that estimated by a single climatological station. This information on the dynamics and mechanisms of overwintering provides insight that should be helpful in formulating improved predictive models, risk assessments, and management strategies of boll weevils.

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